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Global affiliation of juvenile fishes and invertebrates with mangrove habitats

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ABSTRACT.—Mangroves are critical fish and invertebrate habitats, however, identifying to what degree species are affiliated to mangrove systems remains challenging. Here we outline and apply two quantitative methods and one qualitative method for assessing the degree of mangrove affiliation globally at a species level, based on habitat-specific fish and invertebrate species densities extracted from an exhaustive search of the literature, for mangroves and their associated coastal habitats. We assessed all 121 species for which we had ≥ 7 mangrove records and, where data allowed, quantified the percent contribution of mangroves to the summed species density across all habitats. We set the threshold for identifying a species as “highly mangrove-affiliated” as $\geq 70\%$ relative density, and examined its validity by subjecting a subset of species either side of the threshold to a thorough review of evidence for mangrove affiliation in the peer-reviewed literature. We found that 53 species were highly mangrove-affiliated, including 24 fish and three invertebrate species from the Atlantic East Pacific (AEP) and nine fish and 15 invertebrate species from the Indo-West Pacific (IWP; two species had global distributions). Thirty-six of the 53 species are of value to artisanal, subsistence, or commercial fisheries (AEP = 21, IWP = 13, Global = 2). While this list of highly mangrove-affiliated species is far from complete due to data limitations, it represents the first attempt to undertake a global overview of highly mangrove-affiliated species, and a proof of concept for a quantitative and objective method of assessment.



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Mangroves provide a nutrient rich and highly structured habitat which dominates many tropical and subtropical estuaries and coastlines. The habitat complexity provided by mangrove forests support increased biodiversity (Gratwicke and Speight 2005) and contributes significant productivity into the systems in which mangroves are found (*see* Hutchison et al. 2014 for a review). Mangroves are also a highly threatened habitat, suffering increasingly high rates of loss globally (Polidoro et al. 2010).

Mangroves provide a wide range of critically important ecosystem services, including shoreline protection, carbon sequestration, water quality regulation, and wood provision (UNEP-WCMC 2005). Mangroves also support fish production, in particular through their role as a nursery habitat (Igulu et al. 2014), by providing juveniles with shelter from predation (Rönnbäck et al. 1999, Laegdsgaard and Johnson 2001) and through increased food abundance (Dittel et al. 1997, Cocheret de la Morinière et al. 2003).

The importance of mangroves in supporting commercial fish catch has been quantified or inferred in several systems (Manson et al. 2005a, Aburto-Oropeza et al. 2008, Carrasquilla-Henao and Juanes 2017). Nevertheless, the degree to which fish and invertebrate species are reliant on mangrove habitats as opposed to the associated estuarine and coastal habitats remains poorly resolved (Lee 2004). Furthermore, the degree to which mangroves increase growth of individuals varies with the habitat setting of the mangrove (Faunce and Serafy 2008a). The inability to disentangle the association between fish and mangroves from other associated habitats, such as seagrasses (Nagelkerken et al. 2001) or the estuaries themselves (Lee 2004, Manson et al. 2005b), has contributed to a number of unsubstantiated claims about the importance of mangroves to fisheries (Sheaves 2017).

There have been many efforts to quantify the association between individual fish and invertebrate species and mangroves, but quantification of the magnitude of this effect is largely missing (*but see* Pantallano et al. 2018). Understanding whether or not mangroves are important during any single life history stage of a species, and indeed which species this may be the case for, is critical in moving forward the debate regarding the role of mangroves as fish habitat, and for quantifying the contribution of the nursery function of mangroves to fish catches. Previous efforts to quantify mangrove dependency [sic] have relied on comparing the abundance of species in the presence or absence of mangroves (Nagelkerken et al. 2001, Pantallano et al. 2018). Such efforts represent a valuable contribution to research regarding mangroves as fish habitat, but there are a limited number of locations where such a paired presence/absence of mangroves can be applied. Therefore, there is a need to develop alternative methods to determine the importance of mangrove habitats to fish and invertebrate species.

Here we present a method for quantifying the degree to which species in mangrove regions are affiliated with mangrove habitats during their juvenile life stage (fishes) or throughout their lives (resident molluscs and decapods), using a global data set. We assess the threshold of relative abundance above which there is strong evidence of a high degree of mangrove affiliation. “Highly mangrove-affiliated species” include species which are fully mangrove dependent (i.e., do not typically occur in any other habitat) as well as species that are consistently found as juveniles at highest densities in mangrove habitats where that option is present (but may use alternative habitats where mangroves are absent). The methodology outlined does not consider all life history stages for fishes and nonresident invertebrates and therefore does not imply a sole dependence on mangrove habitats. Indeed, we acknowledge the importance of a range of accessible nearshore habitats for ontogenetic shifts in some species, which are not captured in this methodology (e.g., Nagelkerken et al. 2000).

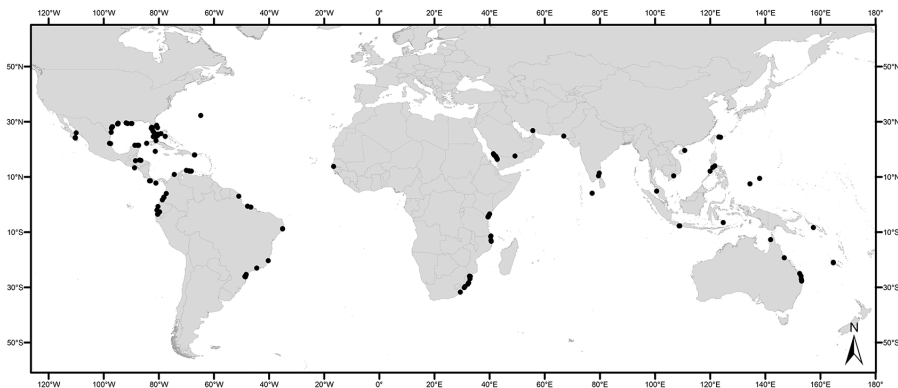


Figure 1. Map of the location of studies from which juvenile fish and invertebrate data were extracted. Basemap; Global Administrative Areas (2018). GADM database of Global Administrative Areas, v3.6. [online] URL: www.gadm.org.

METHODS

A large-scale review of the published literature was undertaken to identify studies containing quantitative, habitat-specific fish and invertebrate densities from mangrove regions of the world. Mangrove regions were identified using the global map of mangrove forests produced by Giri et al. (2011). A database of fish and invertebrate densities derived from 263 publications was compiled, yielding 13,414 species records with a broad geographic spread (Fig. 1). Densities represented a variety of shallow coastal habitats, including mangrove, mud flat, sand, seagrass, saltmarsh, macroalgal beds, oyster, rocky, coral reef, and open water habitats. Mangrove data were selected so as to represent the mangrove habitat as opposed to the broader system. While a small number of studies ($n = 13$) included sampling 5–50 m from the mangrove edge, the vast majority represented in-mangrove sampling or sampling within 5 m of the mangrove fringe. We included sampling 5–50 m from the fringe in situations where mangrove creeks and small estuaries were sampled and mangrove was the dominant habitat type. While the data set was dominated by in-mangrove sampling, we deemed that it was appropriate to include these near-mangrove studies, as some species associated with mangroves are known to have similarly sized home ranges (Dorenbosch et al. 2004, Verweij et al. 2007). If insufficient detail was provided within the publication to determine the exact location of sampling, we deferred to the judgement of the authors, i.e., including sampling that the authors explicitly stated was from mangrove areas. In order to standardize the data set, sampling methodologies which are commonly known to have low catch efficiencies such as vessel-operated trawls, block nets, and fyke nets were excluded from the database. Methods that were included covered visual transects, throw and drop traps, seines, lift nets, and quadrats. The resulting database contained species-specific densities by habitat, standardized to individuals per 100 m².

As mangrove areas are primarily viewed as being critically important for fish and invertebrate species during early life history stages (Igulu et al. 2014) and because ontogenetic shifts are commonly known to occur in mangrove-affiliated species (Serafy

et al. 2015), we further cleaned the data set to represent, as much as possible, only juvenile individuals. This allowed for assessment of the degree of mangrove affiliation during the life history stage when the mobile species are most likely to be critically associated with mangroves. The data set was limited to representing juvenile individuals either through the inclusion of sampling methodologies known to be heavily biased toward small individuals, or by extracting the mangrove-affiliated juvenile size classes where size classes were provided. All size classes were included for resident mangrove invertebrate species such as mangrove cockle, *Anadara tuberculosa*, and mangrove crabs (e.g., *Scylla serrata*, *Ucides* spp., and *Uca* spp.). Sampling for these species is highly specific and there is significant evidence of their reliance on and residence in mangroves throughout most of their life history (Diele 2000, Mackenzie 2001). As such, it was deemed appropriate to include the densities of these species across multiple size classes.

Only species represented seven or more times in the mangrove habitat within the database were included to ensure that there was adequate information available to make a globally relevant assessment. Of the 1389 species recorded in mangroves, 121 fulfilled the criteria of ≥ 7 samples (Supplementary Online Material 1). Of the 121 species, 39 were native to the Indo-West Pacific (IWP), 78 to the Atlantic East Pacific (AEP), and four had a global distribution. While previous studies have confidently inferred species association with mangrove habitats based on the total absence of a species in the absence of mangroves (e.g., Pantallano et al. 2018), assessing the strength of affiliation to mangrove habitat specifically (as opposed to across a landscape of habitats) requires that a lower threshold of association be set. This is because even species which are documented to be highly mangrove associated (e.g., *Monodactylus argenteus*) typically move around within the estuarine or coastal landscape and may therefore occasionally be sampled in nearby alternative habitats (Lugendo et al. 2005).

Three methods were applied in turn to the final fish and invertebrate density data set (Fig. 2). In the first method, the data set was filtered to represent only studies where mangroves were sampled alongside at least one other habitat (i.e., paired habitat studies). Species represented by at least three paired habitat samples in this data set were then assessed for their degree of mangrove affiliation using Equation 1. Species were considered highly mangrove-affiliated if their mean density in mangroves represented $\geq 70\%$ of their mean density summed across all habitats represented [following the Dorenbosch et al. (2005) approach of calculating habitat association]. The second method was applied to all species with three or more records from nonmangrove habitats (no pairing necessary with the ≥ 7 mangrove samples), represented in at least two independent studies. Again, Equation 1 was applied and 70% was considered the threshold above which species can be considered highly mangrove-affiliated. The third method sought to encompass all species which had sufficient records in mangrove areas, but not sampled frequently enough in nonmangrove areas to reliably apply either of the first two methods (Supplementary Online Material 2). In these cases, a literature review of all qualifying species was undertaken to assess the apparent degree of mangrove affiliation. Searches were initially undertaken on Scopus using the scientific species name and “mangrove”. If fewer than five relevant results were returned, the same search was undertaken on Google Scholar. Species were considered highly mangrove-affiliated if there were a minimum of four studies supporting near exclusive use of mangrove habitats with no studies refuting this assertion, or if

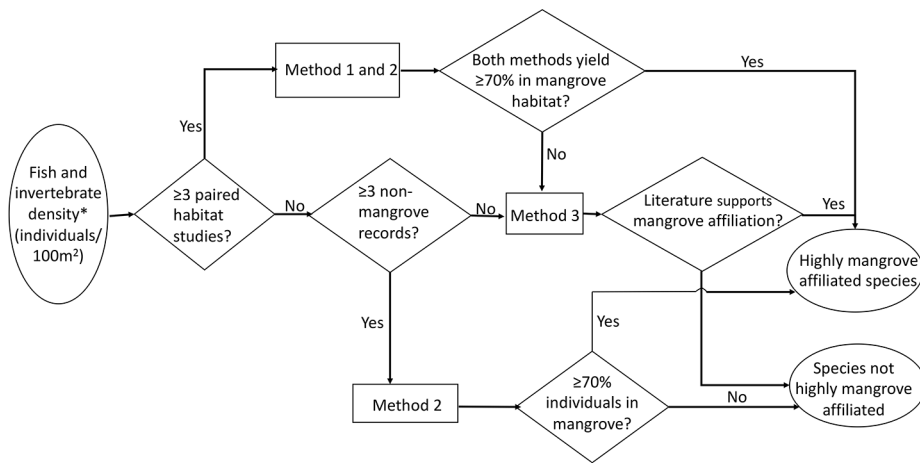


Figure 2. Methodology for assessing whether species commonly found in mangrove areas are highly affiliated with mangroves. * Only species with seven or more mangrove records were assessed.

there were more than ten studies supporting near exclusive use of mangrove habitats and only one suggesting other habitats were preferred. Searches were undertaken in November 2016. Species scoring 60%–70% in methods one and two were also assessed by method three to determine whether 70% was a defensible threshold for concluding a species was mangrove-affiliated (Supplementary Online Material 3).

$$\text{Degree of mangrove affiliation}(\%) = \left(\frac{\text{mean mangrove fish density}}{\text{sum of all habitat fish density means}} \right) \times 100 \quad \text{Eq. 1}$$

Confirmation of the resulting species level mangrove affiliations was sought both internally by comparing methods and externally by seeking expert validation. Firstly, the degree of mangrove affiliation derived by the first and second method was compared for all relevant species. Where the assessments from the first and second methods disagreed (i.e., one assessment found $\geq 70\%$ mangrove affiliation and the other $< 70\%$), a further literature review (method three) was undertaken to determine which assessment had greater support. Finally, the summary of species assessments by all three methods was sent to a panel of nine mangrove fish ecologists with an average of 13 yrs experience sampling in mangroves and representing field experience in the major mangrove regions of the world (excluding West Africa). The experts were asked to propose species they believed to be mangrove-affiliated from their region and to confirm whether the assessments reflected their experience in mangrove and other nearshore habitats. Species flagged by one or more experts were again subjected to literature review and, in the absence of overwhelming evidence, the species was considered not to be highly mangrove-affiliated ($n = 1$).

Species profiles were compiled for the species found to be highly mangrove-affiliated. Species ranges were assigned to the IWP or AEP, *sensu* Alongi (2002), or global distribution. The functional group of each species was determined from FishBase (for fin-fish) or SealifeBase (for invertebrates), and species were assigned omnivore, detritivore, piscivore, invertivore, herbivore, or planktivore feeding groups, respectively. Where the databases provided insufficient information, primary literature was searched using Google Scholar ($n = 5/121$). Finally, we searched the IUCN Red List for species status.

RESULTS

Of the 121 species assessed by at least one of the three methods (Supplementary Online Material 1), 53 were found to be highly mangrove-affiliated (Table 1). These include 24 fish and three invertebrate species from the AEP, and nine fish and 15 invertebrate species from the IWP. The remaining two highly mangrove-affiliated fish species had global distributions. The highly mangrove-affiliated species represented 35% and 62% of the species assessed in the AEP ($n = 78$) and IWP ($n = 39$) regions, respectively.

Thirty-seven species were well enough represented in paired studies to be assessed by method one. Of the 37 species confirmed by method one, 31 were found to produce the same result when method two (using all data) was applied. Of the six species which produced conflicting results between method one and method two, five were confirmed by literature review to be highly mangrove-affiliated (method three). Thirty-nine species were assessed by method two alone, while 45 species were represented in the database by mangrove records alone, or with insufficient numbers of records from other habitats, and therefore underwent a literature review (method three) to determine the degree of mangrove affiliation.

Four species scored $\geq 60\%$ and $< 70\%$ mean relative density in mangrove habitats using method one, of which one (*Mulloidichthys martinicus*) was already included as highly mangrove-affiliated through method two, and confirmed by method three. The remaining three species were subjected to a literature review and found not to be highly mangrove-affiliated (Supplementary Online Material 3). Eight species scored $\geq 60\%$ and $< 70\%$ mean relative density in mangrove habitats using method two, of which two had already been found not to be highly mangrove-affiliated in the assessment from method one. The remaining six were assessed by method three, of which five were not associated with mangrove habitats, and one (*Chloroscombrus chrysurus*) was found to have insufficient data to draw a conclusion (Supplementary Online Material 3).

With all but one exception (*Abudefduf saxatilis*), the expert review agreed with the inclusion of the identified species as being highly mangrove-affiliated (see Supplementary Online Material 1). Expert opinion, however, identified a further 61 species which they believed to be mangrove-affiliated, but which failed to be represented in our data set due to a lack of data (Supplementary Online Material 4).

The mangrove-affiliated species encompass species from all major feeding groups including piscivores, invertivores, herbivores, planktivores, and detritivores (Table 1). The families Haemulidae and Gerreidae (AEP), and Lutjanidae (AEP and IWP) were well-represented in terms of number of highly mangrove-affiliated species, while for invertebrates this was the case for terrestrial crabs (AEP and IWP), and shrimp and gastropods (IWP).

Of the 53 species identified, 36 species are harvested in artisanal, subsistence, or commercial fisheries (AEP = 21, IWP = 13, global = 2). While a significant number of the species were not assessed in the IUCN species Red list ($n = 20$, $n = 1$ data deficient), three of the fish species from the AEP are currently listed as Near Threatened, while one, *Lutjanus cyanopterus*, is listed as Vulnerable (Table 1).

Table 1. List of the 53 species assessed as highly mangrove-affiliated ($\geq 70\%$ of total abundance). Range classed as either Atlantic East Pacific (AEP), Indo West Pacific (IWP), or global. Feeding groups classed as: piscivore (P), invertivore (I), herbivore (H), detritivore (D), planktivore (Pl), or omnivore (O). Species which are known to be targeted by artisanal and subsistence fisheries are noted as harvested. IUCN status given in parentheses with species name if classed as Near Threatened (NT) or Vulnerable (VU); all other species were not assessed, least concern, or data deficient. Habitat association is noted if the species is benthic or terrestrial. All other species have neritic and/or pelagic lifestyles.

Species	Feeding group	Habitat association	Harvested species
AEP — Fishes			
<i>Achirus lineatus</i>	P, I		
<i>Caranx latus</i>	P, I		yes
<i>Centropomus undecimalis</i>	P, I		yes
<i>Cetengraulis edentulus</i>	Pl		yes
<i>Chaetodipterus faber</i>	O (Pl, I, D)		yes
<i>Chaetodon capistratus</i>	I		
<i>Diapterus auratus</i>	O (H, D, I)	neritic/benthic	yes
<i>Eucinostomus currani</i>	O (H, I, D)		
<i>Gerres cinereus</i>	I		yes
<i>Haemulon flavolineatum</i>	I		yes
<i>Haemulon parra</i>	P, I		
<i>Haemulon sciurus</i>	P, I		yes
<i>Lophogobius cyprinoides</i>	O (H, I)	benthic/neritic	
<i>Lutjanus analis</i> (NT)	P, I		yes
<i>Lutjanus apodus</i>	P, I		yes
<i>Lutjanus cyanopterus</i> (VU)	P, I		yes
<i>Lutjanus fulviflamma</i>	P, I		yes
<i>Lutjanus griseus</i>	O (P, I, Pl)		yes
<i>Lutjanus jocu</i>	P, I		yes
<i>Lutjanus synagris</i> (NT)	P, I		yes
<i>Mulloidichthys martinicus</i>	I	benthic/neritic	yes
<i>Scarus guacamaia</i> (NT)	H		yes
<i>Sparisoma rubripinne</i>	H		yes
<i>Stegastes leucostictus</i>	O (I, Pl)	benthic/neritic	
AEP — Invertebrates			
<i>Anadara tuberculosa</i>	D	benthic	yes
<i>Ucides cordatus</i>	H, D	terrestrial	yes
<i>Ucides occidentalis</i>	H	terrestrial	yes
IWP — Fishes			
<i>Atherinomorus lacunosus</i>	Pl		yes
<i>Gerres filamentosus</i>	I		yes
<i>Lutjanus argentimaculatus</i>	P, I		yes
<i>Lutjanus argentiventris</i>	P, I		yes
<i>Lutjanus russellii</i>	P, I		yes
<i>Monodactylus argenteus</i>	Pl, D		yes
<i>Siganus canaliculatus</i>	H		yes
<i>Sillago sihama</i>	I		yes
<i>Terapon jarbua</i>	O (P, I, H)		yes
IWP — Invertebrates			
<i>Cerithidea decollata</i>	D	benthic	
<i>Fenneropenaeus indicus</i>	O (D, Pl, I)	benthic	yes
<i>Fenneropenaeus merguensis</i>	P, I	benthic	yes
<i>Littoraria intermedia</i>	H	terrestrial	
<i>Littoraria pallescens</i>	H	terrestrial	
<i>Littorina scabra</i>	H, D	terrestrial	
<i>Metaplex elegans</i>	I	benthic	
<i>Neosarmatium meinerti</i>	H	terrestrial	yes
<i>Penaeus monodon</i>	I	benthic	yes
<i>Scylla serrata</i>	P, I	benthic	yes
<i>Terebralia palustris</i>	D	benthic/terrestrial	
<i>Uca annulipes</i>	D	benthic/terrestrial	
<i>Uca forcipata</i>	D	benthic/terrestrial	
<i>Uca inversa</i>	D	benthic/terrestrial	
<i>Uca urvillei</i>	D	benthic/terrestrial	
Global — Fishes			
<i>Chanos chanos</i>	O	pelagic/neritic/benthic	yes
<i>Sphyraena barracuda</i>	P, I		yes

DISCUSSION

We present here a quantitative method for assessing the degree of mangrove habitat affiliation of juvenile fish and invertebrate species in mangrove regions of the world. Furthermore, we propose a threshold relative density, above which there is strong and consistent evidence that species are highly mangrove-affiliated. While the data set was restricted to species which were found in mangroves seven or more times, it is nevertheless notable that 44% of the species which were well enough represented to include in the assessment were identified as highly mangrove-affiliated. The resulting list represents a starting point for understanding the importance of mangrove habitats to individual species at a global scale.

Where the quantitative methodology (Eq. 1) was applied, it appeared to function well. Only one species identified as highly mangrove-affiliated was deemed not to be following expert review and confirmation in the literature. Furthermore, of six species (out of 37) returning different assessments of mangrove affiliation from method one and method two, only one species was found not to be highly mangrove-affiliated following a thorough literature review. This implies that if either method determines that $\geq 70\%$ of the total density of individuals is found in mangroves, that species is likely to be highly mangrove-affiliated. Using a single method alone may result in false negatives and produce a conservative assessment of highly mangrove-affiliated species. Methods one and two are fully quantitative and, where data are available, provide a less intensive and more transparent method for assessing mangrove habitat affiliation than relying on species-specific literature alone.

The application of a 70% threshold in determining when a species is highly mangrove-affiliated performed well. All species which had been identified by both method one and two as being $\geq 60\%$ and $< 70\%$ affiliated were confirmed not to be highly mangrove-affiliated following a literature review (Supplementary Online Material 3). This suggests that when, on average, 70% of individuals are found in mangroves as opposed to other associated habitats, this is strongly indicative of consistent affiliation to mangrove habitats.

Our efforts to create a standardized data set of mangrove fish and invertebrate densities highlight the exceptional species diversity present in these regions, with 1389 species recorded in total in our mangrove data set, while also shedding light on the lack of quantitative data from mangrove habitats, West Africa in particular (Fig. 1). The lack of data resulted in only 121 of the 1389 species recorded in mangroves being assessed, due to the remaining 1268 being represented by fewer than seven mangrove records. Furthermore, of the 121 species, 45 were represented in too few non-mangrove nearshore habitats to allow for methods one or two and were therefore assessed by literature review (method three) alone. While we are confident that the methodology applied to the assessment of the literature was robust and undertaken with a strict rule-based approach, this is inevitably less quantitative and considerably more time consuming. Of the 45 species assessed by method three alone, 23 (51%) were found to be highly mangrove-affiliated (Supplementary Online Material 1).

The lack of quantitative fish and invertebrate data from mangrove regions has inevitably resulted in many highly mangrove-affiliated species being omitted. In particular, we note that the current analysis should not be considered relevant in West Africa due to a near complete dearth of data. The lack of data from many mangrove regions is why we emphasize that the species listed in Table 1 should be considered

a starting point and a proof of concept for the approach used. This is further highlighted by the large number of potentially mangrove-affiliated species identified by mangrove fish experts (Supplementary Online Material 4) which had not been included in the assessment due to a lack of data (Supplementary Online Material 4).

While we believe the approach proposed here provides useful insight into the degree of mangrove affiliation of juvenile fishes, molluscs, and decapods throughout their life history at a large spatial scale, it should be noted that local-scale factors are clearly important in determining the degree of mangrove habitat affiliation in any given location. For example, linkages to other nearby habitats can result in enhanced densities of species with ontogenetic habitat shifts (Nagelkerken et al. 2001), and seasonality can determine the degree of mangrove affiliation (Faunce and Serafy 2008b). There are species included by our assessment as highly mangrove-affiliated (e.g., *Sphyrna barracuda*) which are highly mobile and able to associate with other habitats in the absence of mangroves. We nevertheless believe that our assessment has correctly identified *S. barracuda* as highly mangrove-affiliated. It has been previously noted that juvenile *S. barracuda* show a preference for mangrove habitats where they are present (De Sylva 1963, Nagelkerken et al. 2000), and there is evidence of the direct benefit this species derives from association with mangroves through shelter and increased prey density, particularly during their early life stage (De Sylva 1963, Blaber 1982). Nevertheless, the inclusion of this species also highlights the fact that being highly mangrove-associated is not equivalent to complete dependence on the habitat. Similarly, we emphasize that not all species which benefit from the presence of mangrove habitats would be identified as highly mangrove-affiliated.

Despite species from the AEP having greater representation in the final data set than species from the IWP (AEP = 78, IWP = 39), similar numbers of species were found to be highly affiliated with mangroves in both regions (27 and 24 species, respectively). A meta-analysis by Igulu et al. (2014) found that juvenile fish densities were higher in mangroves than in seagrasses and coral reefs in the Caribbean, relative to the IWP. The authors postulated that differences in salinity and tidal amplitude between the regions were the likely driver. While the studies are not directly comparable as we focused only on the relative mangrove densities in this study, our findings appear to contradict those of Igulu et al. (2014), as we find that a greater proportion of fish species were highly mangrove-affiliated (as opposed to affiliated to other habitats including seagrasses) in the IWP relative to the AEP (AEP = 24 of 75, IWP = 9 of 21). Invertebrates included in the database were overwhelmingly found to be highly mangrove-affiliated in both regions (AEP = 3 of 3, IWP = 15 of 18).

In many mangrove regions of the world, fishing remains an important source of employment in local communities, predominantly through subsistence or artisanal harvest, as commercial harvests tend to take place further offshore (Hutchison et al. 2014). Thirty-seven of our 53 highly mangrove-affiliated species are harvested, highlighting the importance of mangrove habitats in not just altering fish communities, but also in contributing to fisheries catches, both in mangrove areas and offshore. Invertebrate fisheries can be particularly important locally in mangroves (e.g., Kosuge 2001, Capistrano and Lopes 2012). All three of the highly mangrove-affiliated invertebrate species in the AEP are important artisanally harvested species where they are found. *Ucides cordatus*, for example, is a critical artisanal fishery in mangrove areas of Brazil, with annual landings (1997–2003) of 1200 t from the Caeté Estuary in Pará alone (Diele et al. 2005), while about 15,000 artisanal fishers engage

in mangrove cockle (*Anadara* spp.) collection throughout their Central and South American range (Mackenzie 2001). In contrast, only five of the 15 highly mangrove-affiliated invertebrate species in the IWP are harvested. This, however, includes three commercially valuable penaeid shrimps (*Fenneropenaeus indicus*, *Fenneropenaeus merguensis*, and *Penaeus monodon*). As an indication of value of these fisheries, the shrimp fishery (primarily *F. merguensis*) in Bintuni Bay, Indonesia alone is worth over US \$6 million annually (Ruitenbeek 1994). The fish species identified as highly mangrove-affiliated similarly represent a large number of harvested species, many of which are also important. Eleven of the 29 highly mangrove-affiliated fish species belong to the snapper family (Lutjanidae), which is artisanally, commercially, and recreationally important. This group also represents two species near threatened and one species vulnerable to extinction as assessed in the IUCN red list.

Quantifying and communicating the contribution of mangrove habitats to society may play a key role in combating their continued conversion. Numerous studies have highlighted the data deficiencies in understanding the value of mangroves and how these values vary across geographies (Hutchinson and Philipp 2015, Himes-Cornell et al. 2018). While supporting fish and invertebrate production is well understood to be a critical ecosystem service provided by mangroves, the degree to which individual species rely on mangrove habitats remains significantly debated (Sheaves 2017). We acknowledge that our list of highly mangrove-affiliated species is far from complete, but it provides one approach to quantifying the importance of mangroves to fish communities and associated fisheries. The method presented here can be expanded by increasing the data set to include grey literature not touched on in this effort, as well as the growing data on mangrove fish and invertebrate densities in the future, to allow for an efficient process of determining which species are highly mangrove-affiliated.

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LITERATURE CITED

- Aburto-Oropeza O, Ezcurra E, Danemann G, Valdez V, Murray J, Sala E. 2008. Mangroves in the Gulf of California increase fishery yields. *Proc Natl Acad Sci USA*. 105(30):10456. <https://doi.org/10.1073/pnas.0804601105>
- Alongi DM. 2002. Present state and future of the world's mangrove forests. *Environ Conserv*. 29(3):331–349. <https://doi.org/10.1017/S0376892902000231>
- Blaber SJM. 1982. The ecology of *Sphyrna barracuda* (Osteichthyes: Perciformes) in the Kosi system with notes on the Sphyrnidae of other Natal estuaries. *S Afr J Zool*. 17:171–176. <https://doi.org/10.1080/02541858.1982.11447799>
- Capistrano J, Lopes P. 2012. Crab gatherers perceive concrete changes in the life history traits of *Ucides cordatus* (Linnaeus, 1763), but overestimate their past and current catches. *Ethnobiology and Conservation*. 1:7. <https://doi.org/10.15451/ec2012-8-1.7-1-21>

- Carrasquilla-Henao M, Juanes F. 2017. Mangroves enhance local fisheries catches: a global meta-analysis. *Fish Fish.* 18:79–93. <https://doi.org/10.1111/faf.12168>
- Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, Hemminga MA, Huiskes AHL, Van der Velde G. 2003. Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. *Mar Ecol Prog Ser.* 246:279–289. <https://doi.org/10.3354/meps246279>
- De Sylva DP. 1963. Systematics and life history of the great barracuda, *Sphyræna barracuda* (Walbaum). *Stud Trop Oceanogr.* 1:1–179.
- Diele K. 2000. Life history and population structure of the exploited mangrove crab *Ucides cordatus cordatus* (Decapoda: Brachyura) in the Caete Estuary, North Brazil. PhD Thesis. Zentrum für Marine Tropenökologie-ZMT.
- Diele K, Koch V, Saint-Paul U. 2005. Population structure, catch composition and CPUE of the artisanally harvested mangrove crab *Ucides cordatus* (Ocypodidae) in the Caeté estuary, North Brazil: indications for overfishing? *Aquat Living Resour.* 18(2):169–178. <https://doi.org/10.1051/alr:2005018>
- Dittel AI, Epifanio CE, Cifuentes LA, Kirchman DL. 1997. Carbon and nitrogen sources for shrimp postlarvae fed natural diets from a tropical mangrove system. *Estuar Coast Shelf Sci.* 45(5):629–637. <https://doi.org/10.1006/ecss.1996.0228>
- Dorenbosch M, Grol MGG, Christianen MJA, Nagelkerken I, van der Velde G. 2005. Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on adjacent coral reefs. *Mar Ecol Prog Ser.* 302:63–76. <https://doi.org/10.3354/meps302063>
- Dorenbosch M, Verweij MC, Nagelkerken I, Jiddawi N, van der Velde G. 2004. Homing and daytime tidal movements of juvenile snappers (Lutjanidae) between shallow-water nursery habitats in Zanzibar, Western Indian Ocean. *Environ Biol Fishes.* 70:203–209. <https://doi.org/10.1023/B:EBFI.0000033336.10737.f5>
- Faunce CH, Serafy JE. 2008a. Growth and secondary production of an eventual reef fish during mangrove residency. *Estuar Coast Shelf Sci.* 79(1):93–100. <https://doi.org/10.1016/j.ecss.2008.03.006>
- Faunce CH, Serafy JE. 2008b. Selective use of mangrove shorelines by snappers, grunts, and great barracuda. *Mar Ecol Prog Ser.* 356:153–162. <https://doi.org/10.3354/meps07231>
- Giri C, Ochieng E, Tieszen LL, Zhu Z, Singh A, Loveland T, Masek J, Duke N. 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. *Glob Ecol Biogeogr.* 20(1):154–159. <https://doi.org/10.1111/j.1466-8238.2010.00584.x>
- Gratwicke B, Speight MR. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J Fish Biol.* 66(3):650–667. <https://doi.org/10.1111/j.0022-1112.2005.00629.x>
- Himes-Cornell A, Grose SO, Pendleton L. 2018. Mangrove ecosystem service values and methodological approaches to valuation: where do we stand? *Front Mar Sci.* 5:376. <https://doi.org/10.3389/fmars.2018.00376>
- Hutchinson J, Philipp DP, Claussen JE, Aburto-Oropeza O, Carrasquilla-Henao M, Castellanos-Gallindo GA, Costa MT, Daneshgar PD, Hartmann HJ, Juanes F, et al. 2015. Building an expert-judgement based model of mangrove fisheries value. *Trans Am Fish Soc.* 83:17–42.
- Hutchison J, Spalding M, zu Ermgassen P. 2014. The role of mangroves in fisheries enhancement. The Nature Conservancy and Wetlands International. 54 p.
- Igulu MM, Nagelkerken I, Dorenbosch M, Grol MGG, Harborne AR, Kimirei IA, Mumby PJ, Olds AD, Mgaya YD. 2014. Mangrove habitat use by juvenile reef fish: meta-analysis reveals that tidal regime matters more than biogeographic region. *PLOS ONE.* 9(12):e114715. <https://doi.org/10.1371/journal.pone.0114715>
- Kosuge T. 2001. Brief assessment of stock of mud crabs *Scylla* spp. in Matang Mangrove Forest, Malaysia and proposal for resources management. *Jpn Agric Res Q.* 35:145–148. <https://doi.org/10.6090/jarq.35.145>
- Laegdsgaard P, Johnson C. 2001. Why do juvenile fish utilise mangrove habitats? *J Exp Mar Biol Ecol.* 257(2):229–253. [https://doi.org/10.1016/S0022-0981\(00\)00331-2](https://doi.org/10.1016/S0022-0981(00)00331-2)

- Lee SY. 2004. Relationship between mangrove abundance and tropical prawn production: a re-evaluation. *Mar Biol.* 145(5):943–949. <https://doi.org/10.1007/s00227-004-1385-8>
- Lugendo BR, Pronker A, Cornelissen I, de Groene A, Nagelkerken I, Dorenbosch M, van der Velde G, Mgaya YD. 2005. Habitat utilisation by juveniles of commercially important fish species in a marine embayment in Zanzibar, Tanzania. *Aquat Living Resour.* 18(2):149–158. <https://doi.org/10.1051/alr:2005016>
- Mackenzie CL. 2001. The fisheries for mangrove cockles, *Anadara* spp., from Mexico to Peru, with descriptions of their habitats and biology, the fishermen's lives, and the effects of shrimp farming. *Mar Fish Res.* 63:1–39.
- Manson FJ, Loneragan NR, Harch BD, Skilleter GA, Williams L. 2005a. A broad-scale analysis of links between coastal fisheries production and mangrove extent: a case-study for north-eastern Australia. *Fish Res.* 74(1–3):69–85. <https://doi.org/10.1016/j.fishres.2005.04.001>
- Manson FJ, Loneragan NR, Skilleter GA, Phinn SR. 2005b. An evaluation of the evidence for linkages between mangroves and fisheries: a synthesis of the literature and identification of research directions. *Oceanogr Mar Biol Annu Rev.* 43:483–513.
- Nagelkerken I, Kleijnen S, Klop T, van den Brand RACJ, Cocheret de la Morinière E, van der Velde G. 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. *Mar Ecol Prog Ser.* 214:225–235. <https://doi.org/10.3354/meps214225>
- Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, Van't Hof T, den Hartog C. 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuar Coast Shelf Sci.* 51(1):31–44. <https://doi.org/10.1006/ecss.2000.0617>
- Pantallano ADS, Bobiles RU, Nakamura Y. 2018. Dependence of fish on subtropical riverine mangroves as habitat in the Ryukyu Islands, Japan. *Fish Sci.* 84(4):613–625. <https://doi.org/10.1007/s12562-018-1202-9>
- Polidoro BA, Carpenter KE, Collins L, Duke NC, Ellison AM, Ellison JC, Farnsworth EJ, Fernando ES, Kathiresan K, Koedam NE, et al. 2010. The loss of species: mangrove extinction risk and geographic areas of global concern. *PLOS ONE.* 5(4):e10095. <https://doi.org/10.1371/journal.pone.0010095>
- Rönnbäck P, Troell M, Kautsky N, Primavera JH. 1999. Distribution pattern of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Philippines. *Estuar Coast Shelf Sci.* 48:223–234. <https://doi.org/10.1006/ecss.1998.0415>
- Ruitenbeek JH. 1994. Modelling economy-ecology linkages in mangroves: economic evidence for promoting conservation in Bintuni Bay, Indonesia. *Ecol Econ.* 10(3):233–247. [https://doi.org/10.1016/0921-8009\(94\)90111-2](https://doi.org/10.1016/0921-8009(94)90111-2)
- Serafy JE, Shideler GS, Araújo RJ, Nagelkerken I. 2015. Mangroves enhance reef fish abundance at the Caribbean regional scale. *PLOS ONE.* 10(11):e0142022. <https://doi.org/10.1371/journal.pone.0142022>
- Sheaves M. 2017. How many fish use mangroves? The 75% rule an ill-defined and poorly validated concept. *Fish Fish.* 18(4):778–789. <https://doi.org/10.1111/faf.12213>
- UNEP-WCMC. 2005. In the front line: shoreline protection and other ecosystem services from mangroves and coral reefs. UNWP-WCMC.
- Verweij MC, Nagelkerken I, Hol KEM, van den Beld AHJB, van der Velde G. 2007. Space use of *Lutjanus apodus* including movement between a putative nursery and a coral reef. *Bull Mar Sci.* 81:127–138.

